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RESPONSE OF A BIRD ASSEMBLAGE IN SEMIARID CHILE TO THE 1997–1998 EL NIÑO

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ABSTRACT.—The semiarid region of Chile is influenced by El Niño Southern Oscillation. Its absence causes droughts and its presence causes wet years, which in turn result in variations in resource levels for avian assemblages. We show that bird species richness and density follow some of these pulses closely. Sixty-one bird species, 32 of which were Passeriformes, were sighted during five years in Las Chinchillas National Reserve (300 km N of Santiago). Overall, 30 species (49%) were residents and 31 (51%) were migratory. The most speciose trophic groups were insectivores (34%), carnivores (28%), and granivores (25%). Bird species richness and density declined from 43 species and 45–50 individuals/ha in spring 1993, to 29 species and 15–20 individuals/ha in autumn 1996. Increases were observed with the onset of El Niño, reaching totals of 42 species (a 45% increase from 29) and densities of 55–60 birds/ha in summer 1997. Similar trends were observed in one of two major food resources measured: small mammals. Positive correlations were found between raptor species richness and density and small mammal density, but not between insectivorous bird species richness or density and terrestrial arthropod abundance. Because the climate was very dry during most of the time of our study, we may have witnessed the lowest boundary for species richness and bird density. Whether the 1997–1998 El Niño brought the maximum bird species richness and density for the site is yet to be seen. *Received 20 Jan. 1999, accepted 2 June 1999.*

Bird assemblages vary through time in species composition and absolute and relative abundances, in the short term (seasonal, Avery and van Riper 1989), medium term (between years, Wiens 1990a, b), or both. Most authors agree that this variation reflects changes in the resource base, mainly food (Feinsinger et al. 1985, Wiens 1993). Three factors are generally proposed to account for how birds use resources (Pearson 1991): competition (Martin 1987, Pulliam and Dunning 1987), predation (Lima 1987), and physical or abiotic stresses (Karr and Freemark 1983). The degree to which these factors determine bird assemblages is controversial (Loiselle and Blake 1991). Although they are not mutually exclusive, these three factors are usually assessed individually, rarely two simultaneously (Martin 1985, Kotler and Holt 1989). Most attention has concentrated on the role of species interactions rather than on physical factors (Pearson 1991), although arguably the latter set the stage for biotic interactions.

The periodic intrusion of El Niño Southern Oscillation along the western coasts of the Americas constitutes a major physical disturbance that brings warm water to the shores and increased precipitation to the adjacent land masses. Although initially studied in its oceanographic and climatic aspects, increased awareness of the multiple effects of El Niño is shifting the focus to the effects of this phenomenon on birds (Barber and Chavez 1983, Schreiber and Schreiber 1984, Gibbs and Grant 1987, Grant and Grant 1987, Hall et al. 1988, Miskelly 1990, Massey et al. 1992, Lindsey et al. 1997). Previous studies dealt with the putative El Niño effects on seabird colonies or on terrestrial island birds. Effects on inland birds have been little studied.

The semiarid areas of northcentral Chile (27–32° S), apart from seasonal fluctuations in weather and food resources, are characterized by medium term fluctuations in rainfall (Fuentes et al. 1988). Accordingly, plant cover, amount of herbage production, and size of seed bank vary markedly among years (Gutiérrez et al. 1993). Small mammals track these food resources closely (Jiménez et al. 1992) and perhaps arthropods do also (Fuentes and Campusano 1985). It has become increasingly clear that the unusual rainfall brought by El Niño events to semiarid Chile are responsible for increased primary productivity, which in turn leads to population outbreaks of small mammals and to local increases in the populations of carnivorous birds that prey on them (Meserve et al. 1995; Jaksic et al. 1996, 1997).

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Interestingly, no multi-year studies have been conducted on the response of an entire bird assemblage in such semiarid areas to changes in precipitation, or in primary (vegetation) or secondary production (mammals, arthropods). Here we report upon the effect of variation in such secondary production on bird species richness and density.

STUDY AREA AND METHODS

Study area.—The study site is located inside Las Chinchillas National Reserve (simply called the reserve hereafter), at 31° 30′ S, 71° 06′ W, about 300 km N of Santiago, Chile, and 60 km E of the Pacific coast. The reserve spans 400–1700 m elevation, has a rugged topography, and is dominated physiographically by an alternation of ridges and ravines, with few flat areas between. The climate is classified as semiarid by di Castri and Hajek (1976), with sporadic precipitation concentrated during Austral winter months (June through August). Mean annual rainfall 1986–1997 was 170 mm, but with marked increases in 1987 (513 mm), 1992 (307 mm), and 1997 (367 mm) associated with the respective El Niño events (1986–1987, 1991–1992, 1997–1998). Two dominant landscape types characterize the study site: ravines and slopes. Ravines are more vegetated (70.3% shrub cover) than slopes (52.7% cover).

Vegetation.—The vegetation is a thornscrub composed mainly of spiny dicots, bromeliads, and cacti (details in Gajardo 1978). Dominant species in ravines are *Stevia* sp. (15.5% cover), *Colliguaya odorifera* (12.5%), *Pleocarphus revolutus* (6.6%), *Baccharis paniculata* (5.4%), *Proustia cuneifolia* (5.4%), and *Maytenus boaria* (5.2%). Dominant species in slopes are *Bahia ambrosioides* (16.9%), *Proustia cuneifolia* (19.3%), *Baccharis paniculata* (8.6%), *Porlieria chilensis* (8.0%), *Lobelia polyphylla* (4.0%), and *Puya berteroniana* (3.0%).

Census techniques.—During the four calendar seasons of every year from July (winter) 1993 to January 1998 (summer), we conducted fixed band transects to census birds (Burnham et al. 1980, Conner and Dickson 1980, Bibby et al. 1993). One transect was in a ravine (1500 × 20 m = 3 ha, time spent = 45–55 min/transect) and another in a southern exposure mid-slope (500 × 40 m = 2 ha, 20–30 min/transect) of each El Cobre and El Grillo creek beds (sampling effort = 4 transects/season, the two creek beds combined). The two ravine transects were surveyed throughout the study period, but the two on slopes were terminated in the summer of 1995. The two creek beds were dry except for the wet winter of 1997, but are hereafter called creeks nonetheless. Transects were started 1 h after the sun's rising above the top of ridges east of the two creeks. Diurnal raptors (Falconiformes) were censused opportunistically in a 2000 ha area centered around the two creeks. The abundance of the four nocturnal raptor species (Strigiformes) at the site was assessed based on responses to playbacks of their calls (Johnson et al. 1981, Haug and Didiuk 1993) 0.5 h after the first star was spotted in the sky. Every playback was broadcast for 1 min for each species sequentially, at four fixed stations located in the ravine of the El Cobre creek, at two stations in the ravine of El Grillo creek, and at two stations in the bottom of the cliffs that border the Aucó stream. For the Strigiformes, we considered the area sampled to be about 2000 ha, and all estimates of abundance refer to the minimum number of individuals detected. All densities are standardized as the number of individuals per species per hectare.

Bird categorizations.—Bird nomenclature follows Meyer de Schauensee (1982). We categorized species according to their reproductive status, diet, residence status, and habitat. Reproduction: birds were classified as either nesting or non-nesting at the site, depending on whether they were observed actually nesting. Some cryptic nesters may have escaped our detection and thus the number of nesting species may be underestimated. Diet: we followed Jaksic and Feinsinger (1991) in establishing the following primary diets: carnivores, insectivores, granivores, nectarivores, frugivores, folivores, and omnivores. These categorizations come from the literature or from direct observation. Residence: we considered a species to be resident at the study site if it was observed on 13 (ca 70%) of the 19 visits to the site. A species was categorized as migrant, either if it stayed at the site only during spring and summer (summer visitor) or if it stayed only during autumn and winter (winter visitor). Habitat: the following landscape units were considered as "habitats": ravines (bottom of creeks), slopes (sides of creeks), flat areas, and water edges (around permanent streams).

Food availability.—Small mammal density was assessed during five days/four nights trapping bouts in each season on opposite slopes of El Cobre creek. Each of the two grids consisted of a 7 × 7 arrangement of stations at 15 m intervals equipped with one Sherman live trap at each station. Total trapping area was 2.2 ha. Jiménez and coworkers (1992) provided details of this trapping scheme. Terrestrial arthropods were sampled with Barber pitfall traps (Southwood 1978) consisting of a 200 ml plastic vial with its rim at ground level, inside of which a 100 ml plastic vial was tightly fitted and filled with water and biodegradable detergent. One hundred such traps were placed at El Cobre creek along four transects with stations at 10 m intervals. Two transects were on opposite slopes and had 20 traps each; two transects (with 30 traps per transect) were in the ravine. Specimens were collected at 24 h intervals during two consecutive days and their total abundance expressed as individuals per trap per 24 h. This total abundance was weighted by the proportion of traps placed in each habitat type (2:3, slopes:ravine). Unlike the case for mammals, this method provides information only on relative densities of large terrestrial arthropods through time.

Statistical analyses.—To determine whether there were associations between habitat and bird densities through time, we compared data obtained in the two slopes with those from the two ravines because these were the two physiognomically most salient landscape features in the reserve. The degree of association between bird densities and two food resources (mammals and arthropods) was determined separately for carnivorous (Falconiformes and Strigiformes) and insectivorous birds by Spearman correlation coefficients (Sokal and Rohlf 1981). Because raptor sightings could not be assigned unequivocally to either slopes or ravines (as they apparently hunted in both habitat types), these data were pooled. In the case of insectivorous birds, we could assign sightings unequivocally to one or the other of the two habitats, and thus we were able to make separate comparisons with arthropod abundance in either slopes or ravines. Bird and arthropod densities were compared by means of Wilcoxon matched-pairs tests (Sokal and Rohlf 1981). The results from Barber traps may be considered only as approximations of terrestrial arthropod density. We did not sample aerial or foliage arthropods. All statistical analyses were performed with software Systat version 7.0 for Windows 95.

RESULTS

Characterization of the bird assemblage.—We sighted 61 species during our 5 year study (Table 1), 32 (53%) of which were Passeriformes. Thirty species (49%) were residents (but only 13 species were sighted in all 19 visits). Transient species were equally divided between winter visitors (10%) and summer visitors (10%). Another 31% of the species were sighted too few times to enable us to categorize them, save as accidentals or occasionals. Two species were not observed but known to be present. The White-tailed Kite (*Elanus leucurus*) had been sighted previously (Jaksic et al. 1996) and thus we categorized it as a migrant. We considered the Great Horned Owl *Bubo virginianus* to be resident, despite having detected it during only five visits because we collected freshly regurgitated pellets at each visit (Jaksic et al. 1996).

In terms of species numbers, the best represented trophic groups were insectivores (34%), carnivores (28%), and granivores (25%), accounting for 87% (53 species) of the local assemblage (Table 1). Thirty-eight (62%) of the 61 species nested in the reserve, including three summer visitors: Aplomado Falcon (*Falco femoralis*), Giant Hummingbird (*Patagona gigas*), and White-tufted Tyrant (*Elaenia albiceps*; Table 1). Seventy-seven percent of the species were sighted in ravines, 54% on slopes, 11% on flat areas, and 7% near small streams and ponds. (These percentages add to more than 100% because some species visit more than one habitat type; Table 1.) Bird densities were not different, either between the two ravines (Wilcoxon matched-pairs test; $Z = 0.283$; $n = 19$; $P > 0.05$) or between the two slopes ($Z = 0.891$; $n = 11$; $P > 0.05$). Thus, we felt justified to analyze our data from the two creeks by habitat type only.

Multi-year trends.—Drought conditions prevailed during the first four years of our study (1993–1996); rainfall ranged 40–106 mm compared to a mean of 170 mm for 1986–1997 (Fig. 1). By contrast, 1997 had over twice the mean annual precipitation recorded for the study site (Fig. 1). Concomitantly, there was a declining trend in bird species richness from 43 species in winter 1993 to 29 at the end of the drought in autumn 1997 (a 33% decrease; Fig. 1). Twenty-nine species may well represent the minimum number of bird species present in the reserve at any time. As soon as El Niño driven precipitation reappeared at the site (the previous two occurrences were 1987 and 1992), there was an increase from 29 species in autumn 1997 to 42 species in summer 1997 (a 45% increase; Fig. 1). Whether this is close to the maximum bird species richness that the site can accommodate has not been determined.

Bird density also tracked precipitation patterns (Fig. 2). Bird numbers in ravines declined from about 45–50 individuals/ha (1993) to about 10/ha in summer 1994 (the driest year in the series; Fig. 1), and started a slow recovery through 1995 and 1996, reaching densities of 55–60 birds/ha during summer 1997. Bird densities on slopes were apparently less than those in ravines (Fig. 2) but paralleled the same trends until summer 1995, when we terminated censuses on slopes.

Similar trends were observed among small mammals but not among terrestrial arthropods (Fig. 3). Small mammals declined markedly through 1993 and 1994, remained at very low levels 1995–1996, and recovered after the spring 1997 (Fig. 3). Terrestrial arthropods did not display such marked fluctuation (Fig. 3). There were significant positive correlations between small mammal density and both raptor species richness ($r_s = 0.77$, df = 17, $P < 0.001$) and raptor density ($r_s = 0.76$, df = 17, $P < 0.001$). Although positive, there were no

TABLE 1. Birds of Las Chinchillas National Reserve (northcentral Chile) and their categorization by reproductive status, dietary category, residence status (in parentheses, number of calendar seasons the species was sighted), and habitat type (landscape aspect).

Species	Reproduction	Diet	Residence	Habitat
Nothoprocta perdicaria	Nesting	Granivore	Resident (18)	Ravine/Slope
Casmerodius albus	Non-nesting	Carnivore	Migrant (6)[a]	Water edge
Egretta thula	Nesting	Carnivore	Migrant (8)	Water edge
Nycticorax nycticorax	Non-nesting	Carnivore	Migrant (1)	Water edge
Vultur gryphus	Non-nesting	Carnivore	Migrant (5)	Slope
Elanus leucurus	Non-nesting	Carnivore	Migrant (0)[b]	Flat areas
Geranoaetus melanoleucus	Nesting	Carnivore	Resident (16)	Ravine/Slope
Buteo polyosoma	Nesting	Carnivore	Resident (14)	Ravine
Parabuteo unicinctus	Non-nesting	Carnivore	Migrant (8)	Flat areas
Milvago chimango	Nesting	Insectivore	Resident (14)	Ravine/Flat areas
Falco peregrinus	Non-nesting	Carnivore	Summer visitor (5)	Ravine/Slope
Falco femoralis	Nesting	Carnivore	Summer visitor (4)	Slope
Falco sparverius	Nesting	Insectivore	Resident (13)	Ravine/Flat areas
Callipepla californica	Nesting	Granivore	Resident (19)	Ravine/Slope
Rallus sanguinolentus	Nesting	Carnivore	Migrant (8)	Water edge
Vanellus chilensis	Nesting	Carnivore	Resident (14)	Flat areas
Columba araucana	Non-nesting	Granivore	Winter visitor (3)	Ravine
Zenaida auriculata	Nesting	Granivore	Resident (14)	Ravine/Slope
Metriopelia melanoptera	Unknown	Granivore	Summer visitor (11)	Ravine/Slope
Cyanoliseus patagonus	Unknown	Frugivore	Resident (15)	Ravine
Tyto alba	Nesting	Carnivore	Migrant (11)	Ravine/Slope
Bubo virginianus	Nesting	Carnivore	Resident (6)[b]	Ravine/Slope
Glaucidium nanum	Nesting	Carnivore	Resident (13)	Ravine/Slope
Speotyto cunicularia	Nesting	Carnivore	Resident (16)	Ravine/Slope
Caprimulgus longirostris	Nesting	Insectivore	Resident (19)	Ravine
Patagona gigas	Nesting	Nectarivore	Summer visitor (12)	Ravine/Slope
Sephanoides galeritus	Non-nesting	Nectarivore	Winter visitor (10)	Ravine/Slope
Colaptes pitius	Non-nesting	Insectivore	Migrant (8)	Slope
Picoides lignarius	Nesting	Insectivore	Resident (19)	Ravine/Slope
Geositta rufipennis	Non-nesting	Granivore	Winter visitor (6)	Ravine/Slope
Upucerthia dumetaria	Non-nesting	Insectivore	Migrant (10)	Ravine
Upucerthia ruficauda	Non-nesting	Insectivore	Summer visitor (5)	Ravine
Chilia melanura	Nesting	Insectivore	Resident (19)	Ravine/Slope
Leptasthenura aegithaloides	Nesting	Insectivore	Resident (19)	Ravine/Slope
Asthenes modesta	Nesting	Insectivore	Resident (16)	Ravine/Slope
Pteroptochos megapodius	Nesting	Insectivore	Resident (19)	Ravine/Slope
Scelorchilus albicollis	Nesting	Insectivore	Resident (19)	Ravine/Slope
Scytalopus magellanicus	Nesting	Insectivore	Resident (16)	Ravine
Agriornis livida	Non-nesting	Carnivore	Migrant (7)	Slope
Pyrope pyrope	Nesting	Insectivore	Resident (18)	Ravine/Slope
Muscisaxicola macloviana	Non-nesting	Insectivore	Winter visitor (2)	Ravine/Slope
Elaenia albiceps	Nesting	Insectivore	Summer visitor (7)	Ravine
Anairetes parulus	Nesting	Insectivore	Resident (18)	Ravine/Slope
Colorhamphus parvirostris	Non-nesting	Insectivore	Winter visitor (8)	Ravine
Tachycineta leucopyga	Nesting	Insectivore	Resident (19)	Flat areas
Pygochelidon cyanoleuca	Non-nesting	Insectivore	Migrant (3)	Flat areas
Troglodytes aedon	Nesting	Insectivore	Resident (19)	Ravine/Slope
Phytotoma rara	Non-nesting	Folivore	Migrant (1)	Ravine
Turdus falcklandii	Nesting	Omnivore	Migrant (9)	Ravine
Mimus thenca	Nesting	Omnivore	Resident (19)	Ravine/Slope
Sicalis sp.	Non-nesting	Granivore	Migrant (3)	Ravine
Zonotrichia capensis	Nesting	Granivore	Resident (19)	Ravine/Slope
Sturnella loyca	Nesting	Omnivore	Resident (19)	Ravine
Curaeus curaeus	Nesting	Omnivore	Resident (16)	Ravine/Slope
Phrygilus gayi	Non-nesting	Granivore	Winter visitor (8)	Ravine/Slope

TABLE 1. CONTINUED.

Species	Reproduction	Diet	Residence	Habitat
Phrygilus fruticeti	Nesting	Granivore	Resident (18)	Ravine/Slope
Phrygilus alaudinus	Nesting	Granivore	Migrant (8)	Ravine
Diuca diuca	Nesting	Granivore	Resident (19)	Ravine/Slope
Carduelis uropygialis	Non-nesting	Granivore	Migrant (2)	Ravine
Carduelis barbatus	Non-nesting	Granivore	Migrant (2)	Slope
Passer domesticus	Nesting	Granivore	Migrant (12)	Ravine

[a] Species categorized simply as migrants did not yield enough data to determine whether they are summer or winter visitors, occasionals, or accidentals.
[b] Not sighted during our work, but present in the area. See text for details.

significant correlations between terrestrial arthropod abundance and insectivorous bird species richness (r_s = 0.06, df = 17, $P >$ 0.05), density on slopes (r_s = 0.49, df = 9, P > 0.05) nor density on ravines (r_s = 0.37, df = 17, $P >$ 0.05).

During the transition from drought (1993–1996) to wet year (1997), two previously unrecorded species arrived at the reserve, the folivorous Rufous-tailed Plantcutter (*Phytotoma rara*) and the fish and amphibian eating Brown Heron (*Nycticorax nycticorax*).

DISCUSSION

The percentage (51%) of species at our study site that were migrants, is similar (48% of 88 species) to that reported by Marone (1992a,b) in the Monte scrubland across the Andes at similar latitudes in Argentina. As in Chile, the high percentage of migrants in the

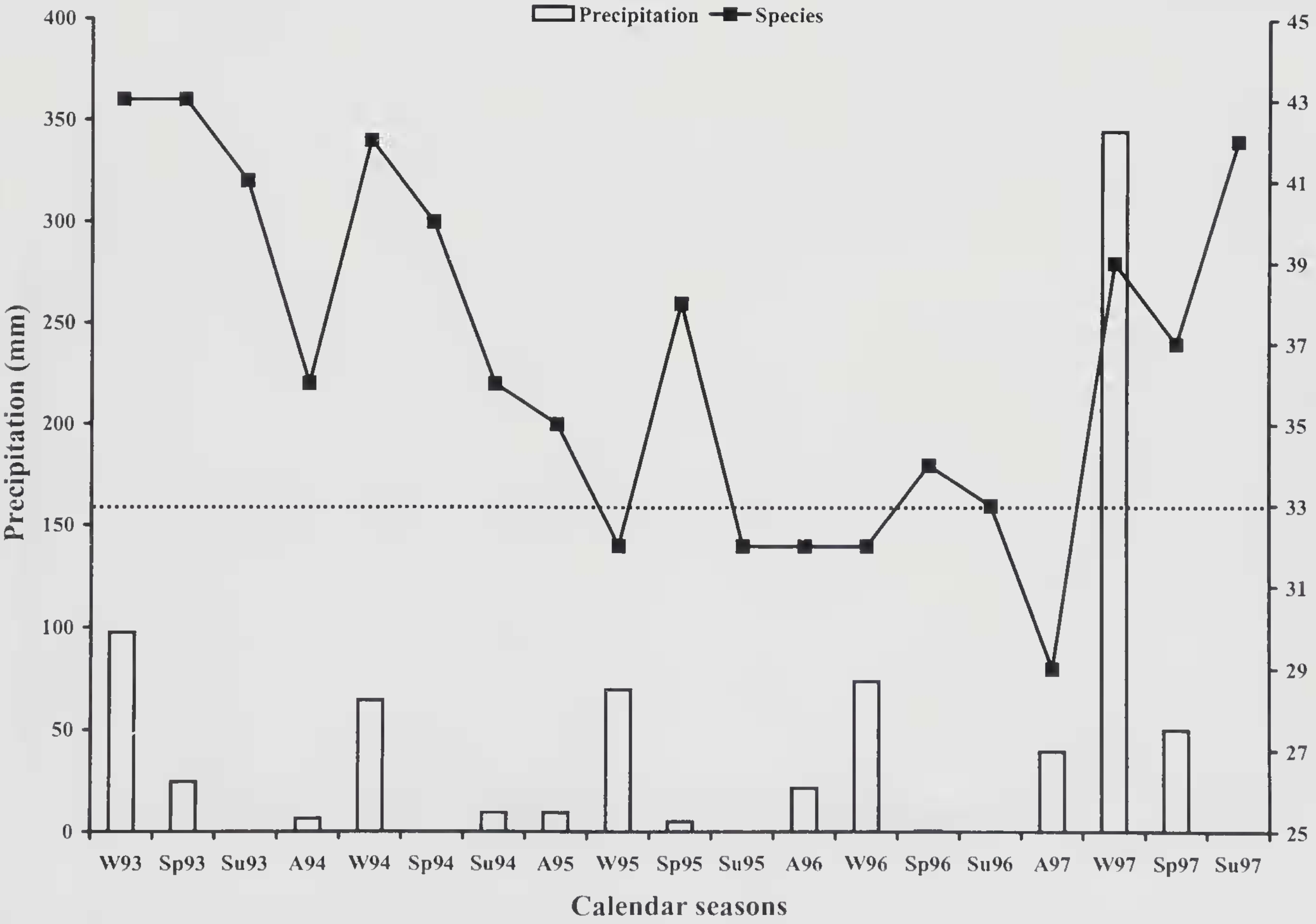

FIG. 1. Seasonal variation in rainfall and number of bird species at Las Chinchillas National Reserve throughout the study period (19 calendar seasons = 5 years). W = Winter (June–August), Sp = Spring (September–November), Su = Summer (December–February), A = Autumn (March–May). The segmented line represents the mean annual rainfall of the last 12 years.

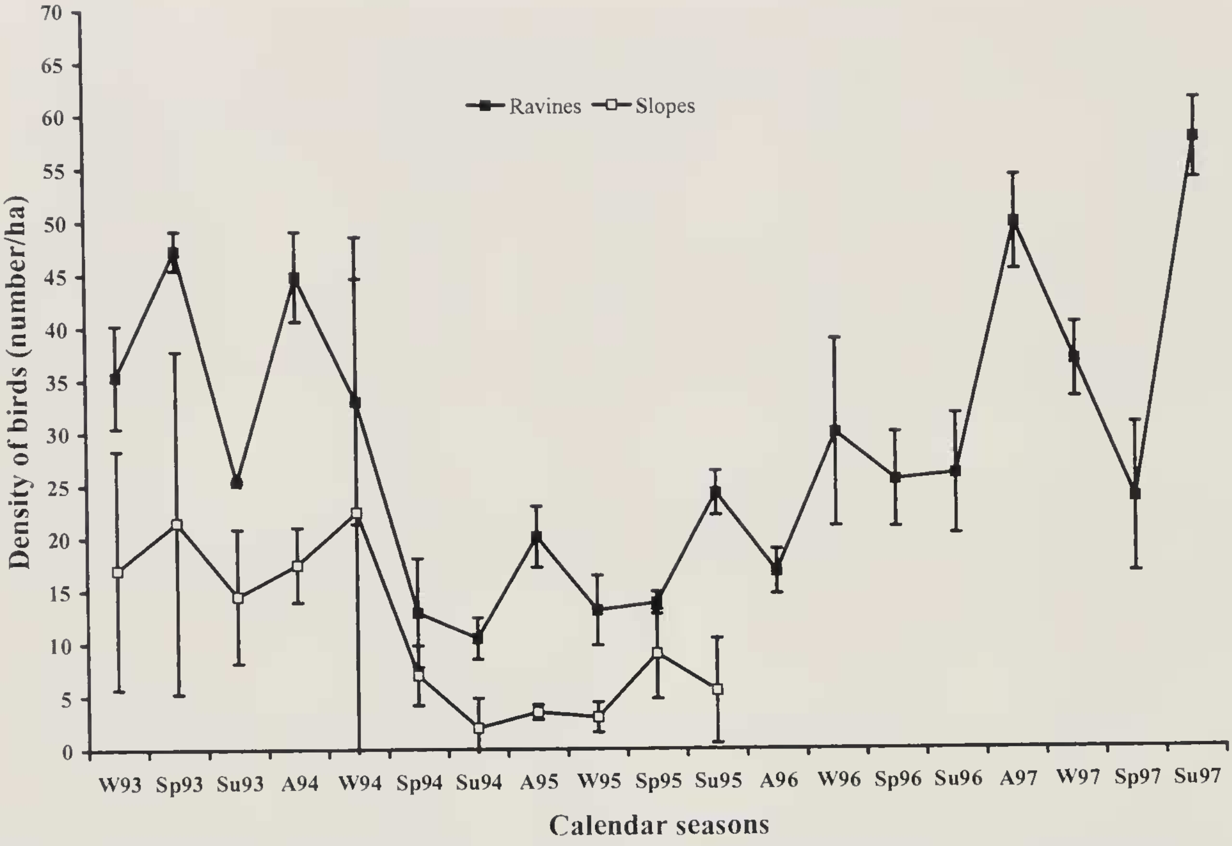

FIG. 2. Bird density (mean ± SD) at the reserve throughout the study period, by habitat type: ravines and slopes. W = Winter, Sp = Spring, Su = Summer, A = Autumn. Censuses on the slopes were discontinued after summer 1995.

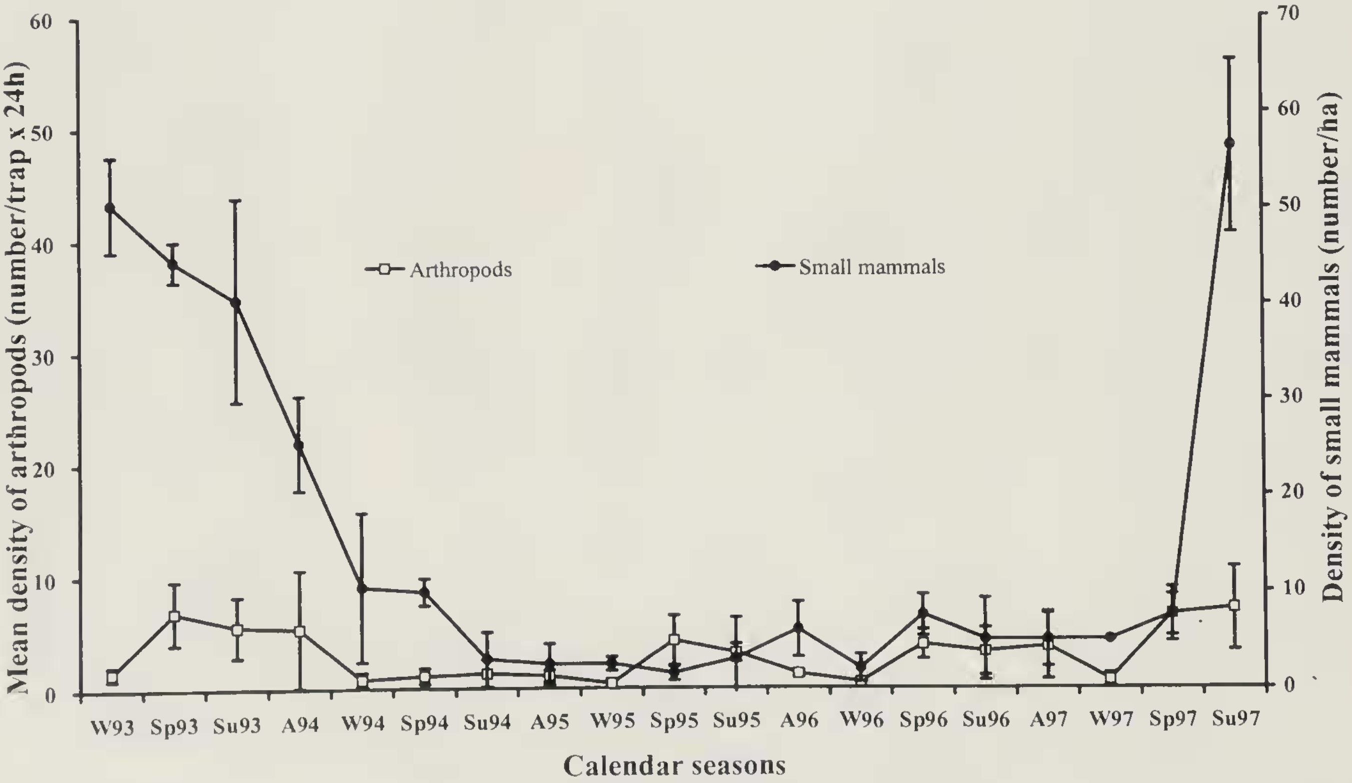

FIG. 3. Abundance of terrestrial arthropods (mean ± SD) and of small mammals (mean ± SD) at the reserve throughout the study period. Abundance of arthropods is the mean of four samples (two from opposite facing slopes and two from a ravine), that of mammals is an average for the north and south facing slopes. W = Winter, Sp = Spring, Su = Summer, A = Autumn.

Argentine Monte may be associated with the extreme fluctuations in precipitation that characterize arid and semiarid regions of South America. Varying precipitation levels in Chile are associated with changes in primary and secondary production (Fuentes and Campusano 1985; Jaksic et al. 1996, 1997). Migrant birds may exploit these unpredictable resources by moving north from the more mesic Mediterranean region of central Chile or down from the Coastal Range to the west or the Andes to the east of our study area.

Marone (1992a,b) observed that insectivores (52%), carnivores (19%), and granivores (15%) dominated the Argentine Monte, accounting for 86% of the local assemblage, similar to the 87% we recorded in Chile. Nevertheless, there were more insectivores and fewer carnivores and granivores in the Argentine site than in our Chilean site. This suggests that there may be differences in resource levels between Chilean and Argentine semiarid sites. More data are needed from the Monte.

We detected positive correlations between number and/or density of bird species and specific resource levels (i.e., with regard to small mammals but not to terrestrial arthropods). Gutiérrez and coworkers (pers. comm.) measured the seed bank of the reserve before (1996) and during El Niño (1997). We found a positive association between this resource and richness/density of granivorous birds during the respective years. In central Chile, López-Calleja (1995) found that the granivorous Diuca Finch (*Diuca diuca*) and Rufous-collared Sparrow (*Zonotrichia capensis*), two species that were also present at our site, changed their seed preferences in response to short-term fluctuations in seed abundance. A detailed study of the abundance of these two species and their respective diets in relation to the seed bank in the reserve is needed.

Why were birds in our study site more abundant in ravines than in slopes? Perhaps food levels are higher in ravines than on slopes. Also, there is more vegetated ground in ravines (70%) than on slopes (53%). Structural aspects of the former habitat may render it more attractive to birds. The presence of a tree layer (e.g., *Maytenus boaria, Quillaja saponaria*) in ravines, which is absent from slopes, may favor higher bird densities because it provides more shelter, roosting and nesting sites, and perhaps greater food diversity (e.g., foliage insects).

The bird assemblage in the reserve showed both short (seasonal) and multi-year variation in its composition and density. Although bird species richness and density in our study site were lower during drought years and higher during wet years, it should be noted that droughts are more frequent and last longer than El Niño events (eight dry years versus four wet ones in 1986–1997). In a semiarid climate, perhaps dry years set the baseline in species richness and density for the bird assemblage, and both increase during wet years because of the immigration of opportunistic species from elsewhere. Thus, El Niño driven rains impose a strong abiotic influence, which cascades from increased primary and secondary productivity to bird species richness and density.

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